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Reassignment of *Chordeiles vielliardi* Lencioni-Neto, 1994, to *Nyctiprogne* Bonaparte, 1857, with comments on the latter genus and some presumably related chordeilines (Caprimulgidae)

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Chordeiles vielliardi was described from two specimens: an adult male and a juvenile male taken near Manga, Bahia (10°23'S, 42°30'W), in the valley of the Rio São Francisco, north-eastern Brazil (Lencioni-Neto 1994). Lencioni-Neto diagnosed it as a 'Caprimulgidae of small size, without white markings on the wing, tail, or throat.' He allocated it to the genus *Chordeiles* and concluded that 'the most closely related species is the sympatric *Chordeiles pusillus*' because of its 'relatively small bill and lack of prominent rictal bristles... proportions near those of *Chordeiles pusillus*... and approaching that species in its pattern, habitat, and behaviour' (translation from description in French). The new species was not tape-recorded and the only vocalization heard, a 'bit-bit' delivered during the day when the birds were flushed from day-roosts, was described as similar to a vocalization of Least Nighthawk *Chordeiles pusillus*.

During the course of field work in November 1994, in the valley of the Rio São Francisco near Januária in northern Minas Gerais (15°31'S, 44°23'W) *c.* 600 km south of Manga, Bahia, the first four authors heard and observed several small nightjars similar to Band-tailed Nighthawk *Nyctiprogne leucopyga*, a species unknown from Minas Gerais or from the valley of the Rio São Francisco. We captured, photographed, measured, then released one individual, and tape-recorded others. These birds lacked

the white median tail-band and white lateral throat patches (the latter being buffy and poorly defined) that mark all known populations of *N. leucopyga*.

We subsequently examined an unidentified caprimulgid specimen deposited in the Laboratory of Ornithology, Universidade Federal do Rio de Janeiro (UFRJ) recovered in April 1994, near Mocambinho, Minas Gerais, by Larissa Cunha, which proved to be the *Nyctiprogne* nighthawk we had observed in that region. Comparison of this specimen with the holotype of *Chordeiles vielliardi* leaves no doubt that the Minas Gerais population is referable to that form. In this paper we re-evaluate the relationships of *Chordeiles vielliardi* based primarily on information lacking in the type description, and discuss generic diagnosis of *Nyctiprogne* relative to other genera in the subfamily Chordeilinae of the Caprimulgidae.

Generic and species status of *Chordeiles vielliardi*

Plumage

We directly compared the holotype of *Chordeiles vielliardi* held at the Museu de Zoologia da Universidade de São Paulo (MZUSP; the paratype had not been deposited in a public institution) with the specimen from near Mocambinho, Minas Gerais (mentioned above) and 22 specimens of *Nyctiprogne leucopyga* held at the MZUSP. This series of *N. leucopyga* includes 15 (six males, eight females and one sex unknown) from the lower Rio Tapajós; four (two males [one a juvenile] and two females) from Conçeição do Araguaia, Pará; two females from Jamundá (Paraná Bom Jardim), Pará (all of the above are presumably nominate *leucopyga*), and the holotype (male) of *N. l. majuscula* (Pinto & Camargo 1952). Though Lencioni-Neto (1994) stated that he compared his specimens of the new species with 'material available at MZUSP and at the Paris au Muséum national d'Histoire naturelle (MNHN)', he provided no data based on these comparisons, and did not list the specimens examined. The comparative measurements provided in his Table II were taken from Ruschi (1979), and most appear to be grossly erroneous.

Nyctiprogne leucopyga has a conspicuous white median band on the three outer rectrices, lacks white in the primaries, and has white on the throat restricted to a small, rounded patch on either side (*contra* the illustration in Meyer de Schauensee & Phelps 1978 reproduced in Hilty & Brown 1986, although the text is accurate in both works). *Chordeiles vielliardi* is almost identical to *N. leucopyga*, differing primarily in lacking the median tail-band. *Chordeiles pusillus* differs dramatically. It is illustrated, and described accurately and concisely, in Hilty & Brown (1986).

Vocalizations

Fig. 1 permits comparison of the songs of (A) *Chordeiles vielliardi* (B) *Nyctiprogne l. leucopyga* (C) *N. l. majuscula* and (D) *Chordeiles p. pusillus*. The songs of *C. vielliardi* and *N. leucopyga* (both the nominate and the geographically closest named population) are strikingly similar in pattern and tonal quality. Each comprises three elements, with the first separated from the other two by a long (*c.* 1.5–2.0 s) pause. The first note is occasionally given repeatedly before the two-element phrase.

Frequency of repetition of the two-element phrase is intra-individually variable, but the two elements are invariably given together. The song and calls of nominate *C. pusillus* bear no resemblance. Recordings of all these taxa may be heard on the compact disc produced by the National Sound Archive of the British Library (Ranft & Cleere 1998).

Habitat and behaviour

Chordeiles vielliardi is most common along the Rio São Francisco where the river is bordered by gallery woodland and brushy growth of this woodland, and is apparently uncommon or absent where this habitat has been removed or highly altered

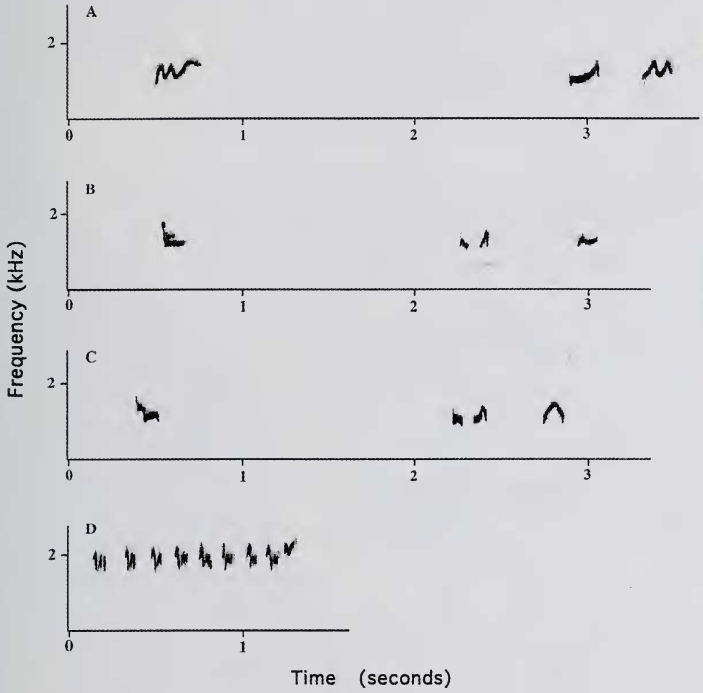

Figure 1. General spectrographic comparison of the songs of (A) *Chordeiles vielliardi* from Januária, Minas Gerais; (B) *Nyctiprogne leucopyga* from Santarém, Pará, Brazil (presumably nominate *leucopyga*); (C) *N. leucopyga* from Poconé, Mato Grosso (presumably *majuscula*); and (D) *Chordeiles pusillus* from Petrolina, Pernambuco (presumably nominate *pusillus*). Note close similarity of flat-frequency, three-element, structure of *Nyctiprogne* taxa in A-C relative to much shorter, rising, multiple-note series of *Chordeiles p. pusillus* (D). Note divergence in note structure between A and B/C, monosyllabic structure of second note of A, and longer interval between first and second notes of A. The degree of intra- and inter-individual variation in these vocalizations needs further study. Samples of each were: *C. vielliardi* (4); *N. l. leucopyga* (8; from the lower rios Tapajós and Xingú); *N. l. majuscula* (3 from Mato Grosso, Brazil including 1 by Jacques Vielliard [Hardy *et al.* 1980 and updates, Ranft & Cleere 1998] and 4 from northeastern Bolivia by Sjoerd Mayer); and *C. p. pusillus* (5 from Pernambuco and Bahia). All recordings except five of the *N. l. majuscula* by BMW.

and semi-arid *caatinga* scrub now dominates the river edge. Loose colonies of up to 30+ birds were found roosting for the day in dense, often brushy vegetation. The birds perched 'crossways' (perpendicular to the substrate) from *c.* 0.2 to 1.5 m above ground, never on the ground (*contra* Lencioni-Neto 1994), sometimes with two to four individuals huddled side-by-side on a thin, horizontal limb. When flushed during the day, individuals flew a short distance to land on another low, horizontal perch, often uttering a short single or double note, which is apparently the vocalization mentioned by Lencioni-Neto (1994).

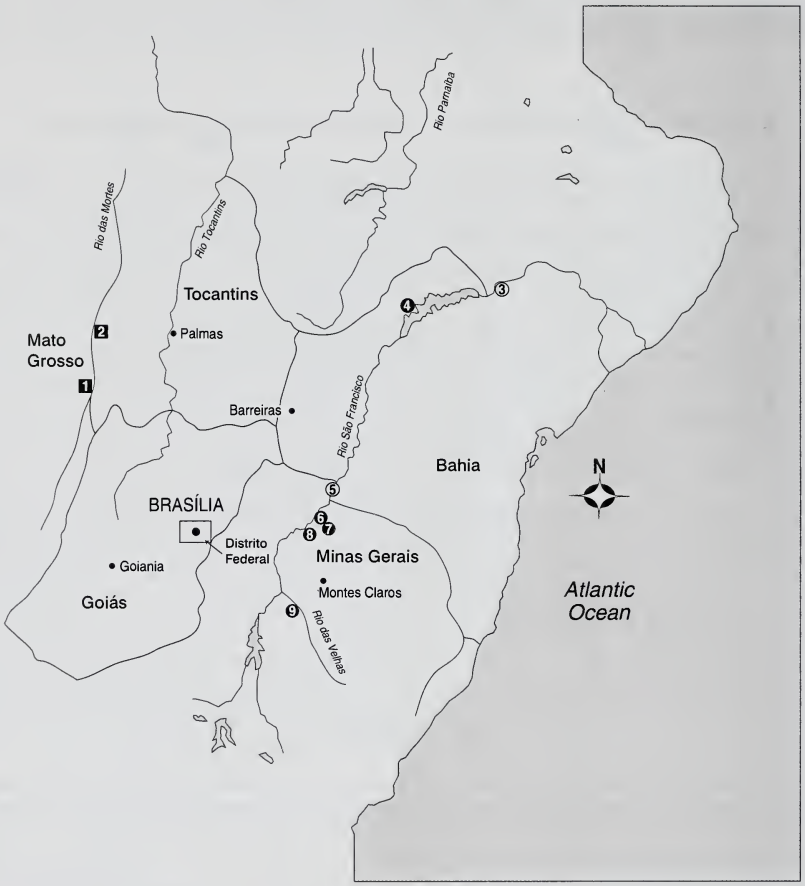

Figure 2. Localities mentioned in the text. 1. The type locality of *Nyctiprogne leucopyga majuscula* (Pinto & Camargo 1952), Dumbá, on the Rio das Mortes, Mato Grosso (14°27'S, 51°01'W). 2. The closest known locality for *N. l. majuscula* to the range of *Nyctiprogne vielliardi* in the valley of the Rio São Francisco, Parque Estadual Ilha do Bananal, Tocantins (09°50–10°50'S, 49°56–50°37'W). 3. Curaçá, Bahia. 4. The type locality of *N. vielliardi* (Lencioni-Neto 1994), near Manga, Bahia. 5. Carinhanha, Bahia. 6–7. Localities close to the village of Mocambinho, Minas Gerais. 8. Januária, Minas Gerais. 9. The Rio das Velhas, near its confluence with the São Francisco, close to Pirapora, Minas Gerais.

Especially on clear days, the birds began to vocalize around sunset, singing from concealed day-roost perches for a short time, usually less than *c.*15 minutes. There was another active song period around dawn. We have never observed *C. vielliardi* singing in flight, but individuals frequently gave various calls (mostly single notes) on the wing, sometimes in an irregular series, mostly soon after leaving or as they were returning to the day roost, and during intraspecific interactions.

Foraging commenced well before dark and was entirely aerial. We witnessed impressive concentrations of foraging birds on several occasions. For example, on 20 December 1999, from a vantage point near Mocambinho, 150-200 individuals were seen along *c.* 300 m of shoreline, foraging over the São Francisco. Individuals flew rather slowly and low, from 1 to *c.* 10 m over the water. Flight characteristics were distinctive, with shallow, fluttery wingbeats interspersed with occasional slightly deeper strokes, and much short-distance gliding with the wings held in a dihedral position. They frequently banked abruptly to roughly retrace their route as they pursued tiny arthropod prey. Foraging groups had dispersed by the time it had become completely dark.

We did not observe any courtship behaviour. On 9 November 1998, GMK located a nesting *C. vielliardi* at Mocambinho, in a sandpit *c.* 2 m wide, 15 m in length, and 2.5 m deep. The nest-site was in the depression of a human footprint close to one edge of the pit and 1 m from a small plant. It held two pinkish eggs. On close approach, the incubating bird flushed to a low perch (30–50 cm high) in nearby *caatinga* scrub.

The above description of *C. vielliardi* accords almost exactly with our field observations of *Nyctiprogne leucopyga.* That species inhabits *várzea* and *igapó* edge and, to a lesser extent, thick brush on dry ground, always in the immediate vicinity of water. It is concentrated almost entirely in 'blackwater' regions, and is thus rare or absent over much of the western Amazon basin. It also occurs locally in the seasonally flooded portions of the Venezuelan *llanos* and the central Brazilian *pantanal.* Day roosts are loosely communal in low, dense vegetation, often with abundant, tangled vines. Cherrie's (1916) fine description of roost sites and behaviour closely matches our own experience:

"During the day these birds conceal themselves in the dense thickets bordering ponds and streams, where they may be found perched on horizontal branches from 30 to 100 cm from the ground. They perch crossways of [i.e., perpendicular to] the branch, and not infrequently I have seen from two to eight or ten huddled close beside one another all facing the same direction."

We have noted *N. leucopyga* perched as high as *c.* 2 m above ground, but never on the ground. The nest-site is situated in a shallow, leaf-lined depression on sandy ground (BMW pers. obs.). Synchronized flight performed by two birds involves turning manoeuvres and short glides in which participants remain within *c.* 0.5 m of each other as one or both emit low, churring sounds. This appears to be an element of courtship.

Chordeiles pusillus differs from *Chordeiles vielliardi* and *Nyctiprogne leucopyga* in several respects. It inhabits seasonally dry, even arid open country, such as savannas, *campinas*, and *caatinga* brush, often far from water. *Chordeiles pusillus*

roosts directly on open ground, usually among camouflaging pebbles and rocks, often several metres from brushy cover. Individuals begin to forage up to 20–30 minutes prior to sunset, attaining heights of 10–50+ m above ground within minutes of leaving the roost. The birds fly with several relatively deep, smooth wing beats followed by a glide, with frequent slight changes in direction, seldom banking sharply or retracing part of the foraging route (unless over an isolated water source, such as a pond or cattle tank). Like its congeners, *Chordeiles pusillus* sings from perches (i.e., the ground) and in flight. While singing on the wing, it sometimes performs a high, shallow-swooping display flight.

Taxonomic conclusions and diagnosis of the genus *Nyctiprogne*

Close parallels in voice, plumage, habitat, and behaviour unequivocally demonstrate that *Chordeiles vielliardi* is a member of the *Nyctiprogne leucopyga* complex, and indicate no particular affinity to *Chordeiles pusillus* or any other member of that genus. Therefore, we propose reassignment of *vielliardi* from *Chordeiles* to *Nyctiprogne*. Within the *Nyctiprogne leucopyga* complex, distinctions in both plumage and vocalizations suggest species status for *Nyctiprogne vielliardi*. Though there appears to be a general reduction in the amount of white in the plumage of *Nyctiprogne* relative to other chordeilines (none in the wing and little in the throat), we view the lack of white in the tail of *vielliardi* as a significant, derived character. We suspect that the rather obvious differences in the sonograms of songs of *N. vielliardi* and *N. leucopyga* (e.g., structure of individual notes and inter-note intervals; Fig. 1A compared to 1B and C) reflect real character divergence. However, documenting the degree of both intra- and (especially) inter-individual variation would ideally involve a larger sample of recordings of better quality.

Since the description of *Nyctiprogne* Bonaparte, 1857, its integrity has not been challenged; in fact, it was clearly supported by Oberholser (1914) and Ridgway (1914). However, considering only Bonaparte's (1857) limited description ("very small bill with somewhat concealed nostrils" *fide* Friedman 1945), one could make a case for merging *Nyctiprogne* with *Chordeiles*. We maintain *Nyctiprogne* based on several distinctions which, in combination, set it apart from other groups within the Chordeilinae. These include small size; lack of sexual dichromatism; lack of white in the wing (which *Lurocalis* also lacks), greatly reduced white in the throat; possession of a conspicuous median tail-band (except for *vielliardi*); habit of singing only from a perch, never in flight; habit of roosting side-by-side (not individually isolated, as do all other chordeilines, notwithstanding grouping of some species); habit of perching 'crossways' on (perpendicular to) thin, low branches (as opposed to parallel orientation on somewhat broader, higher limbs as some *Chordeiles* do and *Lurocalis* always does), never on the ground (as *Chordeiles* and *Podager* frequently do); and distinctively slow, fluttery flight. Some of the flight and perching peculiarities may eventually be linked to modifications of skeletal structure or musculature, which have not been studied. Other distinctions separating *Lurocalis*

are its proportionately short tail and nesting in trees (Straneck *et al.* 1987, Simon & Bustamante 1999).

Nyctiprogne's peculiarities of singing only from a perch and of perching crossways on branches are shared by most of the lowland Neotropical members of Caprimulginae. Differences between *Nyctiprogne* and most Neotropical members of Caprimulginae include *Nyctiprogne*'s reduced rictal bristles, habit of roosting by day above ground (most Neotropical caprimulgines roost on the ground or other terrestrial substrates such as rock walls and cliffs), roosting side-by-side, and foraging exclusively in flight (typical of most chordeilines but not of caprimulgines, all species of which regularly perform aerial sallies from the ground or slightly elevated perches, although some species also make multiple prey attacks during extended, rapid, linear flights). We mention all of this in consideration of the question: Could *Nyctiprogne* be more closely related to some nightjars of the Caprimulginae than to the nighthawks of the Chordeilinae? The two subfamilies differ in several characteristics of cranial morphology (Oberholser 1914); these should be verified for *Nyctiprogne*, which apparently has not been examined in this respect. It seems conceivable that roosting above ground and foraging exclusively in flight by *Nyctiprogne* could be obligatory adaptations to evolution in flooded habitats. In our opinion, systematic placement of *Nyctiprogne* awaits a well-corroborated phylogeny of the Caprimulgidae, or at least one for the Neotropical members of that family. Regardless of its relationship to other members of the family, the genus *Nyctiprogne* is a well-defined evolutionary lineage of widespread distribution and one that has undergone more diversification at the species level than heretofore recognized.

Biogeography and present status

As mentioned above, *Nyctiprogne vielliardi* was known from a single locality in northwest Bahia. Thus far, all of our observations have been considerably farther south in the Rio São Francisco valley of northern Minas Gerais, where we have found it to be common around Mocambinho (initially documented by Larissa Cunha), near Januária, and near Pirapora where the Rio das Velhas joins the São Francisco (although GMK found no *N. vielliardi* at a spot along the São Francisco just SW of Pirapora in mid-Febraury 2002). However, just a short distance downriver at Carinhanha, Bahia, in November 1998, GMK surveyed at both dawn and dusk for *N. vielliardi* but none was found. Much farther downstream on the margins of the São Francisco at Curaçá, Bahia, during February-March 1997 and again in January 2000, JMB searched unsuccessfully for *N. vielliardi* on several occasions.

The type locality, Manga, Bahia, lies between Carinhanha and Curaçá, on the west (left) bank of the São Francisco near the margin of the Sobradinho reservoir. The creation of this huge reservoir in the 1970s destroyed all semideciduous and gallery woodland along that stretch of the river, which encompassed a large percentage of the probable range of *N. vielliardi*. The two Manga specimens were collected in 1987, several years after the São Francisco was dammed. Whether *N. vielliardi* is still present along the margins of the reservoir should be confirmed, but it appears to

be absent a short distance downriver, near Curaçá. How much farther below Manga, Bahia on the São Francisco *N. vielliardi* occurs (or upstream on the Rio das Velhas or other tributaries of the São Francisco) remains to be determined; vast stretches of the river have not been surveyed.

The localities closest to the Rio São Francisco of Bahia and Minas Gerais from which *Nyctiprogne leucopyga* is known are Nazaria, Piauí (*c.* 580 km north in the valley of the Rio Parnaiba) and Dumbá, Mato Grosso (*c.* 1,200 km west in the valley of the Rio das Mortes), the type locality for the subspecies *majuscula*. The known distribution of *Nyctiprogne vielliardi* and the closest known localities for *N. leucopyga* are shown in Fig. 2.

Several avian taxa range from the middle Rio São Francisco to the valley of the Rio Parnaíba in western Piauí, with some also extending west to eastern Goiás. All are considered to be subspecies of more widespread Amazonian/Orinocan species (examples include Rusty-backed Spinetail *Cranioleuca vulpina reiseri*, Greyish Saltator *Saltator coerulescens superciliaris* and Orange-fronted Yellow-Finch *Sicalis columbiana leopoldinae*). Hellmayr (1929) described a specimen of *Nyctiprogne leucopyga* from the Rio Parnaíba collected by Reiser as 'identical with others from Amazonia, French Guiana, and Venezuela', obviously indicating the specimen has a white median tail-band. *Nyctiprogne vielliardi*, then, represents an example of divergence within the São Francisco–Parnaíba region. A small number of taxa are further restricted to the region from the Rio São Francisco west to eastern Goiás (only 2–3 forms have been regarded as species). Willis & Oniki (1991) restricted endemic species of birds here to 'upland *campina–vellozia* scrub zones and the deciduous forest', further specifying that 'no endemic species comes from nearby lowland habitats...'. However, Spix's Macaw *Cyanopsitta spixii* appears to be a 'lowland' endemic of the middle São Francisco in riverine woodlands (C. Yamashita pers. comm., Collar *et al.* 1992), and we suggest that *Nyctiprogne vielliardi* is another. It was included in an "Endemic Bird Area" called "North-east Brazilian caatinga" (EBA 070; Stattersfield *et al.* 1998), which encompasses the type locality and a much larger region of interior north-eastern Brazil. It is now clear, however, that *N. vielliardi* would be included more appropriately in their EBA 074, which centres on wooded habitats along the middle São Francisco River valley. We suggest that the current status of *Nyctiprogne vielliardi* be defined as "Vulnerable", because it is not protected by any conservation area, and it is likely to suffer significant reduction in numbers if the present alarming rate of destruction of riverine habitat in its limited range continues.

Closing remarks

Although identification of skin specimens of caprimulgids at the genus and species levels is straightforward given comparison with museum series, in the case of *Nyctiprogne vielliardi*, superficial similarity to another species in another genus led to an erroneous description. This would probably not have happened if vocalizations had been studied. There is a similar precedent for generic misallocation being

discovered through attention to vocalizations in the Neotropical Caprimulgidae: Pierson (1986) demonstrated that the voices of Yucatan Poorwill *Nyctiphrynus yucatanicus* and Yucatan Nightjar *Caprimulgus badius* had been transposed in the literature since their earliest descriptions. When Hardy & Straneck (1989) studied the vocalizations of probable sister taxa of these species in Central and South America, Pierson's (1986) correction of generic placement was confirmed.

In the highly nocturnal and morphologically conservative Caprimulgidae, loud and distinctive vocalizations play a seminal role in communicating species identities and maintaining pair-bonds. The case of "*Chordeiles*" *vielliardi* serves to underscore that no taxon should be described without presentation of sonograms and bio-acoustic diagnosis of a sample of tape-recordings of the novel form and its presumed closest relatives except, perhaps, under the most extreme circumstances (e.g., Safford *et al.* 1995). These must be recordings of homologous vocalizations and they should be from as close to type localities as possible. LeCroy & Vuilleumier (1992) recommended that voice be included in descriptions of all new species of birds, and this has certainly become the standard in recent years. Vocalizing birds should be collected to provide vouchers for the associated recordings and for other specimens, such as skeletal material, tissue, and stomach contents.

Finally, Lencioni-Neto (1994) did not propose an English or Portuguese name for *vielliardi*. Bahian Nighthawk was introduced by Cleere (1998, 1999) and subsequently employed by Ranft & Cleere (1998) and Holyoak (2001). Caatinga Nighthawk was coined by Stattersfield *et al.* (1998). Neither is quite satisfactory, especially in light of our greatly increased knowledge of the distribution and other aspects of the natural history of this bird. We suggest the name Plain-tailed Nighthawk to call attention to *Nyctiprogne vielliardi*'s most significant, diagnostic plumage character. The Portuguese name Bacurau-do-São-Francisco serves to highlight the restricted range of *N. vielliardi* and to draw attention to this region's remarkable and highly threatened avifauna.

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